ON THE ANATOMY OF THE GENUS ACAPUS, MONTFORT.

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PLATE IX.

This investigation was undertaken at the suggestion of Mr. O. Collett, who, as a resident in Ceylon, was able to collect and preserve specimens of the animals of nearly all the important varieties and species of *Acavus*. The genus, though confined entirely to Ceylon, presents us with a number of species, some of which have several distinct varieties.

It was with a view to the testing of the validity of these species and varieties from an anatomical standpoint that Mr. Collect collected the specimens forwarded to us; he also furnished notes giving a description of the habitat and colour of the living animal in each case.

The animals were preserved in formal, and were in excellent condition, this medium being undoubtedly a better preservative for

many of the Mollusca than spirit.

In order to make a careful comparison of the different species, it was necessary to undertake a detailed examination of the type of the genus, viz. *Acavus hæmastomus* (Linn.); fortunately there were a number of typical examples of this species.

The anatomy of this type has evidently been examined by various observers—Semper, Pilsbry, Binney, and others; but there is no account published that is sufficiently detailed to serve as a basis for comparison with the other varieties and species, which one could only

expect to vary in minute detail.

After a careful examination of several of the species of Acavus one is struck by the almost absolute similarity in the general anatomy of all the forms. There are no conspicuous differences in any of the species, so that a description of the anatomy of any one form will apply equally well to all; any particular variation occurring in an organ will be noted under the description of that structure.

The figure (Pl. IX, Fig. 1) illustrating the general anatomy of *Acavus* was drawn from a specimen of *A. phænix* (Pfr.), merely on account of its large size and beautifully extended and preserved condition. It will be as well to give here a list of the species and varieties of *Acavus* forwarded to us by Mr. Collett, with his notes on

the colour of the living animal and its habitat.

1. Acavus hæmastomus (Linn.).

(a) Several specimens, the shells of which were variously coloured and banded; they all agreed, however, in the colour of the animal being the same.

"Animal yellow, foot dull grey, head and tentacles dark brown. Peristome of every colour from pure white to deep violet.

Hab.—On plantain and coconut stems in the low-lying districts

of the S.W. Province. Sea level."

(b) Var. "Animal rich nut-brown colour all over, tentacles a little paler with yellow bulbs. Peristome always rose colour."

Hab.—Same as the preceding.

(e) Var. melanotragus (Born). "Animal greyish-yellow, foot grey, head and tentacles grevish-brown. Peristome usually black, but often varied with a blotch of pale lilac or white.

Hab.—On coconut and papan trees (Carica papya, Linn.) in the

Galle district, S. Province, Ceylon."

So far as the anatomy of these varieties is concerned, they do not differ from each other except in the number of teeth in a transverse row of the radula, and, very slightly, in the shape of the individual teeth.

2. Acavus Phænix (Pfr.).

(a) Type. "Animal large, coarsely tuberculated, very dark brown colour all over, including the tentacles and bulbs. Peristome black, dark brown, or white.

Hab.—On coconut palms in low-lying maritime districts, sea level."

(b) Var. "Animal light golden brown all over, head a little darker, tentacles golden. Aperture of the shell relatively small. Peristome very variable, but commonly black.

Hab.—On areca palms in Kandy hill-districts (1500–2000 ft.). Not found in maritime parts. The shells of these animals have hitherto been known as varieties of A. phænix; but the latter is exclusively a maritime low-country shell, and the animals are very different."

Mr. Collett seems to regard this form as a distinct species rather than a mere variety of A. phanix. From a careful comparison of the anatomy of this form with that of a typical A. phanix, there does not appear to be adequate grounds for regarding it as other than a mere variety thereof. The radula is of the same type, and the number of teeth in a transverse row fall within the limits of variation which may be assigned to A, phanix (see p. 107).

Moreover, the internal structure of the penis is identically the same

as that of a typical A. phanix.

3. Acavus superbus (Pfr.).

(a) Type. "Animal chocolate, with orange bulbs and tentacles. Peristome white with chestnut margin.

Hab.—On mango and jak trees, high up on the trunk, in damp

shady places. Near the village of Arslena (2000 ft.)."
(b) Var. Grevillei (Pfr.). "Animal light chocolate colour with orange bulbs and tentacles. Peristome black, shell with a rosy apex.

Hab.—On areca palms with A. superbus var. roseolabiata. Lower Ambagamuwa (2000 ft.)."

(c) Var. roseolabiata (Pfr. & Nevill). "Animal light chocolate, tentacles paler with orange bulbs. Exactly resembling A. superbus var. Grevillei, having also the same habitat."

4. Acavus Waltoni (Rv.).

"Animal bluish-black, tentacles grey. Peristome very dark brown or black.

Hab. — Among fallen leaves in forest, Ambagamuwa. Common throughout the Central Province. 2000–4000 ft."

5. Acavus Skinneri (Rv.).

"Animal bluish-grey all over, tentacles grey. Peristome varies from pale brown to deep violet.

Hab.—Haputala forests (5000-6000 ft.). Amongst fallen leaves."

Pattipola, province of Uva, 5000 ft. (Haly).1

6. Acavus Poleii, Collett.

"Animal mouse-colour, head and tentacles paler. Peristome always white.

Hab.—Udagama, Southern Province. 500 ft. On decaying logs

in the forest swamps. A low-country shell."

The shell of this species is frequently covered with algae like the A. hamastomus type. This alga is never found on the shells of A. Waltoni and A. Skinneri.

INTERNAL ANATOMY OF ACAVUS.

The Alimentary Canal (Pl. IX, Fig. 1). The macroscopic features and general arrangement of the alimentary canal very closely resemble the condition obtaining in Helix aspersa, Müll. The jaw is of the oxygnath type, strong, areuate, perfectly smooth, without median or lateral projections. The buccal mass (b.m.) is very muscular, and the radula-sac well developed. The esophagus (o.) arises from the anterior dorsal surface of the buccal mass, and after passing through the nerve-ring, becomes slightly enlarged to form a crop: closely enveloping this structure are a pair of very compact salivary glands (s.g.), which show a tendency to fuse at their anterior extremities. Two fine salivary duets run forward alongside the esophagus and convey the glandular secretion to the pharynx. The stomach (st.) is a large structure bounded by the right and left lobes of the liver, and partially divided into two chambers-a thin-walled portion into which the esophagus opens, and a thicker-walled chamber receiving the right and left bile-ducts from the corresponding lobes of the liver. The intestine (i.) lies imbedded in the left lobe of the liver and follows a course similar to that in Helix. The rectum (r.),

O. Collett: "Contributions to Ceylon Malacology: (2) Description of a new Helicoid Land Shell from the Southern Province": Journ. Ceylon Branch Roy. Asiatic Soc., vol. xv, No. 49, reprint, p. 2.

which occupies the usual position on the right side of the pulmonary sac, is entirely surrounded by a large blood-sinus, from which afferent vessels are distributed to the roof of the pulmonary chamber. The liver (r.l. and l.l.) is divided into right and left lobes, the former enclosing the ovotestis; the latter is subdivided into three lobules, each of which contributes a bile-duct, the three main ducts opening into the left side of the stomach by a single aperture.

Radula.—The radulæ of three species of Acavus have already been figured, viz., A. hamastomus by Pilsbry, A. phanix by Binney, and A. Skinneri by Semper's; since, however, only two or three teeth, at the most, have been represented, I have thought it advisable to refigure them for the purpose of comparison with the radulæ of the

remaining species of this genus.

The teeth are unicuspid, only the mesocone being represented. trace of either ectocone or entocone is visible in any of the teeth, the extreme laterals possessing only a single cusp. The radula of an embryo of A, phanix taken from the egg exhibited no trace of the tricuspid condition in either lateral or marginal teeth, and differed from the radula of the adult only in the size and number of the teeth.

So slight are the differences in the radulæ of the various species of Acavus, that an examination of the figures (Pl. IX, Figs. 2-7) will give a much clearer idea of the specific peculiarities than any detailed

description.

Individual variation in the number of teeth in a transverse row of the radula appears to be a common feature in all the species, though, so far as I can judge from the examination of the radulæ of a limited number of specimens of most of the species, this variation

in number would seem to lie within certain bounds.

In A. hamastomus (Pl. IX, Fig. 2) the central or rhachidian tooth is long and narrow, the reflexed portion and cusp being stout and projecting considerably beyond the middle of the tooth. admedian teeth are provided on their inner (mesial) border with a rounded projection of the upper margin of the base of attachment, which fits into a concavity on the outer border of the preceding tooth. This process is larger and more distinct in some individuals than In addition there is a projection on the base of the tooth, against which the head of the corresponding tooth on the subsequent The base of attachment of the lateral teeth gradually becomes smaller, and the cusp relatively longer, the further the tooth is situated from the middle line. In the marginal teeth this diminution of the base becomes even more marked, whilst there is a tendency for the reduction of the cusp in the extreme marginals, culminating in the entire absence of a cusp in the last two or three

York Acad. Sci., vol. iii (1883-5), p. 92, pl. ii, fig. Q.

Weisen im Archipel der Philippinen, Theil ii, Bd. iii, Land-mollusken (1870), pl. xvi, fig. 5.

Manual of Conchology, ser. 11. vol. ix (1894), p. 153, pl. xlviii, fig. 14.

^{2 &}quot;Notes on the Jaw and Lingual Dentition of Pulmonate Molluscs": Ann. New

teeth in the row. Semper enumerates the number of teeth in a transverse row of the radula of A. hamastomus from 97 to 101; in the specimens that I examined the number varied from 87 to 101. Whether this expresses the extreme range of variation or not, can only be determined after the examination of a greater number of specimens than I had at my disposal. In two specimens of A. hamastomus, var. melanotragus, that I examined, the number of teeth in a row was constant, viz. 97.

The radulæ of A. superbus (Fig. 3) and A. phanix (Fig. 4) are stouter and broader than that of A. hæmastomus, and the individual teeth, though very similar in contour, are larger. The marginal projection on the lateral teeth is more marked in these species, and

in A. phænix attains its maximum development.

In A. superbus the number of teeth in a transverse row varies from 101 to 105, the type form possessing 101 teeth, the variety roscolabiata

103, and the variety Grevillei 105.

A. phanix possesses from 105 to 117 teeth in a row. Binney has figured the teeth of this species, but his drawing is somewhat inaccurate, and was probably made from an old and worn part of the radula.

Taking the three aforementioned species as representative of that sub-group of the genus Acavus of which A. hamastomus is the type, it would appear that as regards the radula, there is a gradual transition of the one species into the other, and that there is a tendency to an increase in the number of teeth in a transverse row, reaching its maximum in A. phænix, but nevertheless foreshadowed in the varieties of A. hamastomus. Coming to that sub-group of Acavus of which A. Waltoni is the type (the subgenus Oligospira of Ancey 2), we find that a similar variation in the number of teeth in a transverse row occurs. The minimum number of teeth present occurs in A. Skinneri (Fig. 5), 73 to 79. The two specimens of A. Waltoni (Fig. 6) examined possessed 103 teeth in each row. The maximum number was reached in A. Poleii (Fig. 7), in one specimen of which as many as 123 teeth were present in a row, though in another only 103 teeth occurred.

These results can be tabulated, and an average dental formula assigned to each of the species of Acavus, as follows:

	Species.	Number of specimens examined.				Limits of variation.	Average radula formula.		
Α.	hæmastomus			9		·87-101°		47-1-47	
A.	superbus			4		101 - 105		51-1-51	
	phœnix			. 5.		105 - 117		55-1-55	
	Skinneri			2		71 - 77		36-1-36	
	Waltoni			2		103		51-1-51	
	Poleii			3		103-123		56-1-56	

The pulmonary sac is large; the collar is very much thickened, and is provided with two well-marked body lobes (Pl. IX, Fig. 1, b.l.);

¹ Op. cit., p. 100.

² Conchologists' Exchange, vol. ii (1887), p. 22.

orifice (p.a.).

these are more conspicuous in some species than others, being especially well developed in *A. Poleii*. The outer wall of the pulmonary sac is very vascular, the blood-vessels being arranged in a very definite order. Their arrangement is constant in all species of *Acavus*.

A large blood-sinus surrounds the rectum and is continuous with the sinus in the collar. From this space the afferent pulmonary vessels (af.v.) arise; they branch extensively, and ultimately break up into a capillary network. Alternating regularly with the afferent vessels and their branches are the efferent pulmonary veins (ef.v.). The two largest of these run direct to the auricle (au.). The smaller of the two vessels collects the aërated blood from the left side of the lung, whilst the larger one, which originates from the right anterior corner of the external wall of the pulmonary sac, collects blood from the middle and portion of the right side of the lung. A few smaller efferent vessels, which collect blood from a portion of the right side of the lung, instead of pouring their contents into the auricle, run to the convex (anterior) border of the kidney, where they break up into capillaries, and, entering the substance of the kidney, form a renal plexus. The renal capillaries reunite to form a single efferent renal vessel, which lies along the concave (posterior) border of the kidney and opens into the auricle very near the apertures of the efferent pulmonary veins.

The pericardium (pc.) is situated in the left posterior corner of the pulmonary chamber, and encloses a well-developed heart. On the right of the pericardium there is a large crescent-shaped kidney (k.). The ureter (u.) arises from the left side of the kidney close to the pericardium; it lies on the convex (anterior) border of the excretory organ and runs along the extreme posterior end of the pulmonary sac, abutting on the visceral mass; it then curves round and follows the straight portion of the rectum for a short distance, opening into the respiratory chamber by an aperture, the urinary pore (u.p.), situated immediately behind one of the posterior efferent pulmonary vessels. The position of this excretory aperture is very constant in all species of Acavas. Up to this point the ureter is a closed tube, but it is continued beyond the renal pore, as an open groove (u.g.), the floor of which is markedly plicated; this groove runs parallel with the rectum, and eventually terminates just in front of the pulmonary

The arterial system exhibits no important modification. The ventricle gives origin to a common aorta, which divides into posterior and anterior branches. The former is distributed to the liver and posterior portions of the alimentary canal. The anterior aorta (a.a.) passes beneath the first coil of the intestine, where it gives off a branch to the posterior portion of the hermaphrodite duct; it is then continued forwards, supplying the genitalia, alimentary canal, buccal mass, etc., with branches. The reproductive organs, on account of their excessive size, receive several arteries derived from the anterior aorta.

The muscular system needs no special description. The retractor muscles, which are large, converge, with the exception of the retractor

of the penis, to a common point, and are all inserted on the columella. The retractor of the buccal mass is closely attached to the tentacular and labial retractors of the left side; it passes through the nervering, under the esophagus, and then divides into three strips; these are inserted on the ventral and lateral borders of the buccal mass. The retractor muscle of the right ocular tentacle passes between the penis and vagina. The retractor of the penis is terminal, and is attached to the left side of the body-wall.

The *pedal gland* is exactly comparable to that of *Helix*. It opens in the usual position below the mouth, and extends back for about

two-thirds the length of the foot.

Nervous system.—The cerebral ganglia (c.g.) are large and close together; they are united together by a very broad commissure, and, with the pleural and pedal ganglia, form a well-marked circumesophageal nerve-collar. The usual nerves are given off from the cerebral ganglia to the anterior portion of the head, branches being distributed to the tentacles, lips, etc. A pair of buccal nerves arise from the anterior border, and are connected with two buccal ganglia, situated ventro-laterally on the esophagus near its junction with the buccal mass; they are united by a short commissure which runs underneath the œsophagus. From these ganglia several nerves arise, and are distributed, some to the buccal mass, others to the œsophagus, and a fine branch accompanies each salivary duct, passing backwards through the nerve-ring and innervating the salivary glands. Nerves are given off from the pedal and pleural ganglia to the foot and bodywall. A large posterior visceral nerve (v.n.) arises from the pleurovisceral mass; it shortly gives origin to a nerve which runs along the dilated portion of the hermaphrodite duct, and is distributed to that structure and to the alimentary canal. The main division of the visceral nerve bifurcates at the posterior end of the body, one branch going to the heart and kidney, the other being distributed to the convoluted portion of the hermaphrodite duet and to the albumen gland.

Reproductive organs.—The genitalia of Acavus hamastomus and A. Skinneri have been accurately figured by Semper, though his description is somewhat meagre. All the species of Acavus are furnished with almost identically similar reproductive organs as far as the external characters go; there is, however, a slight difference observable between the groups represented by A. hamastomus and

A. Waltoni respectively. (Pl. IX, Figs. 1 and 10.)

In the former group the penis (p.) has very much the same calibre throughout, though there is a gradual tapering off towards either end. In the A. Waltoni group the anterior vestibular portion of the penis becomes greatly elongated and constricted, it is thin-walled, and often slightly coiled upon itself. This condition is not so perceptible in A. Poleii (Fig. 11) as in A. Waltoni, though it is perfectly distinct,

Op. cit., pl. xii, figs. 7, 9, 10.

as will be easily seen if Figs. 1 and 11 are compared. In A. Skinneri (Semper, pl. xii, fig. 7) the penis is very much attenuated, and of scarcely larger diameter than the retractor muscle. I at first thought this extreme attenuation of the penis to be due entirely to the immaturity of the specimen, but later, on dissecting some undoubted adults of this species, the same conditions were found to exist.

With the exception of A. Skinneri, the penis in the other forms is of relatively enormous size. Its internal structure is of considerable interest, and is of use for elassificatory purposes, since it constitutes the most striking and constant difference that is observable in all the species. I will, however, defer the description of these differences The retractor muscle of the penis is terminal in position, its distal end being attached to the body-wall on the left side of the animal.

The ovotestis or hermaphrodite gland (Pl. IX, Fig. 1, h.g.) lies imbedded in the right lobe of the liver, and communicates with a very much convoluted hermaphrodite duct (h.d.); this shortly enters the albumen gland (a,q_*) . Lying on the concave border of the albumen gland, and connected with the hermaphrodite duct, is a small rod like body, which I will, for the time being, designate the hermaphrodite caecum (h.c.).

This structure is very constant in all species of Aearus, and, from its invariable presence, would seem to be of some functional Semper has not indicated it in any of his figures of the genitalia of Acavus. It is very closely applied to the albumen gland, and, in preserved specimens, so similar in colour, that it may

easily have been overlooked by him.

Such a structure is by no means unique, but on the contrary appears to be of very common occurrence in terrestrial Pulmonata, for on looking through Binney's 1 figures of the genitalia of terrestrial molluses I was struck by the number of forms possessing a similar structure. In the majority of these figures this appendix is represented as a paired, or bilobed, structure, whilst in Acavus it appears unpaired.

Simroth 2 has figured a similar unpaired organ in the genitalia of Neohyalimax, occupying exactly the same position that it does in

Acavus. He calls the structure a seminal vesiele.

A careful examination of serial transverse sections through this tubular body, however, revealed the paired nature of the structure (Pl. IX, Fig. 9). The two tubes lie side by side, and are enveloped in a common muscle-sheath; they communicate with one another (Fig. 8) before opening into the hermaphrodite duct. Each tube is lined with eiliated epithelium; a few spermatozoa were present in the lumen, but were not sufficiently abundant to suggest that this organ might function as a storing chamber. The albumen gland (a.g.) is

^{1 &}quot;Terrestrial Mollusks and Shells of the United States," vol. v (1878). ² Proc. Malac, Soc. Lond., vol. ii (1896), p. 41, pl. v, fig. 9.

a large structure pouring its secretion into the hermaphrodite duct by two separate openings. On leaving the albumen gland the hermaphrodite duct becomes enormously dilated, and is divided into a thick-walled glandular prostatic portion (pr.) and a thinner-walled distensible portion, the oviduet (ov.d.); the former communicates with a slightly coiled vas-deferens (v.d.), which enters the penis on its posterior end, a little above the insertion of the retractor muscle. The oviduet is then continued on into the vagina (v.g.) and receives the opening of a very short-stalked spermatheea (sp.). There is hardly any trace of an atrium; the penis and vagina, though communicating with a common genital opening, scarcely fuse to form a common genital cloaca.

The structure of the penis, as before mentioned, is of particular interest, inasmuch as the various species of Acavus present appreciable differences with respect to its internal organization. Taking $A.\ hamastomus$ as a type (Pl. IX, Fig. 12), we find, on opening the penis along the mid-dorsal line, two large lateral pilasters (pl.), having their surfaces ridged and corrugated; lying between these folds is a conspicuous furrow bounded by two tumid lips. The two pilasters converge towards the anterior end of the penis, and in this region a thickening of the ventral wall (v.t.) of the penis is noticeable; this

swelling is better developed in other species.

At the posterior end of the penis is a large penis-papilla (p.p.),

at the base of which the vas-deferens opens.

In A. phanix (Fig. 13) three pilasters are present, there being a median dorsal one in addition to the two lateral ones. The penis-

papilla is also much smaller than in the preceding type.

Acavus superbus (Fig. 14) presents a somewhat different structure. There are no definite pilasters, but rather a series of lateral longitudinal ridges which are markedly papillate. The median thickening of the ventral wall of the penis, that was apparent in A. hæmastomus, becomes excessively developed here, and partially overlies the median furrow. The penis-papilla is very small. The penis in A. superbus is, relatively to the size of the animal, much smaller than in either A. hæmastomus or A. phænix.

Equally well-marked differences are observable in the internal structure of the penis of A. Waltoni and that of A. Poleii. In the former (Fig. 15) the walls are beset by longitudinal ridges with a corrugated appearance; there is no definite aggregation of these folds into pilasters, and the penis-papilla is not very conspicuous. This structure approximates most closely to the condition shown in A. phanix, whereas the structure of the penis of A. Poleii more nearly

approaches that of A. hamastomus.

In A. Poleii (Fig. 16) there are two well-marked lateral pilasters, which converge towards the anterior end of the penis; here the median ventral thickening becomes very conspicuous, and forms a thickened ridge. The penis-papilla (p.p.) is also of excessive size.

The penis of A. Skinneri was too small, and not sufficiently well preserved, to make out accurately the characters of its internal

structure.

It will be seen from the description of the anatomy of Acarus, that this genus presents us with a very compact group, no one species of which differs in any marked respect from any other species. Still, sufficient differences exist, especially as regards the genitalia, to enable us to accurately determine the species. The genus is divisible into two sub-groups, represented by the types A. hamastomus and A. Waltoni respectively, the conchological differences of which are more marked than the anatomical. These two sub-groups differ also with respect to their habitat, the former being entirely arboreal, whilst the latter forms are terrestrial, living amongst fallen logs and dead leaves.

The species A. Poleii, founded by Collett, has been regarded as merely a variety of A. Waltoni by other conchologists, but the two forms are quite distinct, and besides differing in the colour of the animal, and the habitat, also present anatomical differences in the structure of the penis, which can scarcely be regarded as less than specifie.

Unfortunately this paper cannot be regarded as complete, since there are two so-ealled species of Acavus of which I have been unable to obtain specimens, viz., A. prosperus (Albers) and A. fastosus (Albers). In addition there are two varieties of A. hamastomus which were not included amongst the specimens sent for examination. These are A. hæmastomus, var. conus, Pilsbry, and var. concolor, Pilsbry. It is extremely unlikely that either of the above species differ in any considerable respect from those of the A. hamastomus group, and it is probable that they are more nearly related to A. hamastomus than any other form.

EXPLANATION OF PLATE IX.

Fig. 1. General dissection of Acavus phanix.

,, 2. Transverse row of teeth from the radula of Acavus hamustomus, c. median tooth; 1, 3, 6-40, etc., are lateral and marginal teeth. The corresponding teeth of the other species have been figured in the same order, except where otherwise indicated by the number of the tooth.

Radula of Acarus superbus. 3. 22

4. phanix. ,, 5. Skinneri. 9 9

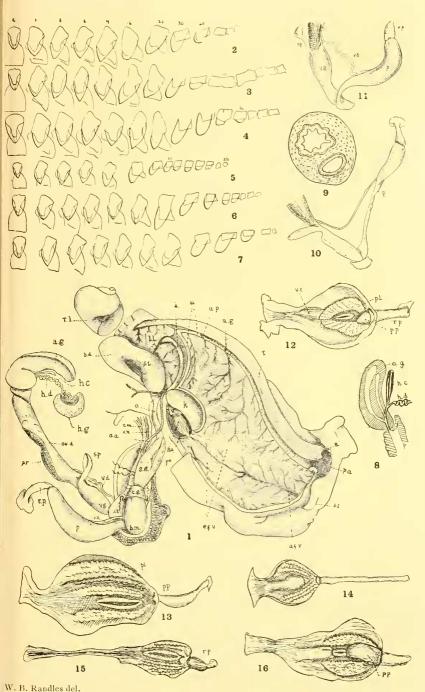
6. Waltoni. 23 7. Poleii. 99

- 8. Diagram representing the hermaphrodite cocum and associated structures, and showing its connection with the hermaphrodite duct. Reconstructed from serial transverse sections.
 - 9. Transverse section through the hermaphrodite excum of Acavus hamastomus.

,, 10. Genitalia of Acavus Waltoni. Anterior part.

,, 11. Poleii.

- Penis of Acavus hamastomus, A longitudinal incision has been made ,, 12. along the mid-dorsal line, and the two halves have been reflected.
- ,, 13. Penis of Acavus phanix. ,, 14.
- ,, ,, superbus, ,, l*ā*. Waltoni.
- ,, ,. 16. Poleii. 2.5



ANATOMY OF ACAVUS.